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Seasonal variability in ecosystem functions: quantifying the contribution of invasive species to nutrient cycling in coastal ecosystems

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Abstract

Benthic ecosystems at temperate and high latitudes experience marked seasonal variation in the environmental factors affecting nutrient remineralization processes both directly and indirectly through their effects on the benthic communities. The invasive polychaete genus *Marenzelleria* spp. represents new functionality in Baltic Sea sediments through its deep burrowing and extensive gallery formation, thus possibly greatly affecting the benthic oxygen and nutrient fluxes. We assessed the seasonal contribution of *Marenzelleria* spp. to fluxes of solutes in monthly field measurements at two sites, 10 and 33 m deep, in the northern Baltic Proper over a year. In general the fluxes of inorganic nutrients and oxygen were higher during summer than during winter and the seasonal variation was more pronounced at the deeper, more biologically active site. By using variation partitioning we were able to demonstrate that *Marenzelleria* and other macrofauna could account for up to 92 % of the variation in the fluxes depending on the site and season. Fauna was the most important in predicting the fluxes in spring when the sediment organic content and the abundance of juvenile *Marenzelleria* spp. were highest, while during e.g. winter the influence of *Marenzelleria* spp., even though abundant, on solute fluxes was negligible. The results from this study have implications for management, and, importantly, for the modelling of nutrient budgets often based on values from studies conducted during the summer period only, thus possibly greatly miscalculating the annual nutrient fluxes.

Key words: nutrient cycling, spionid polychaete, invasion, key species, benthic-pelagic coupling, bioturbation, ecosystem function, seasonality

Introduction

Coastal ecosystems are often diverse, highly productive and intrinsically variable in time and space. In these ecosystems, soft sediments and their associated biota provide a multitude of functions such as nutrient cycling, physical structuring and both primary and secondary production, which constitute important ecosystem services (Snelgrove et al. 2014). Through their sediment reworking and burrow ventilation activities, bioturbating macrofauna oxygenate the sediment, increase the surface available for diffusion, and thereby greatly enhance the exchange of solutes between the sediment and the water column (Vopel et al. 2003, Kristensen et al. 2011). The impact of the macrofauna community on the nutrient cycling depends on e.g. density, biomass and the functional traits of individual species in the community (Mermillod-Blondin et al. 2005) as well as on the physical environment the animals live in, such as sandy or muddy sediment (Braeckman et al. 2014). The activity of the macrofauna also stimulates the activity and growth of the microbial community ultimately responsible for organic matter remineralization (Sundbäck et al. 2004, Foshtomi et al. 2015). Benthic animals also contribute to sediment oxygen consumption through their own respiration and to nutrient dynamics through their own excretion (Vanni 2002).

Coastal ecosystems at temperate and high latitudes often exhibit marked seasonality, which in itself is a strong driver of ecosystem structure and functions such as productivity and nutrient cycling. The Baltic Sea experiences marked seasonal variation in the environmental conditions such as light, temperature and organic matter production (Leppäranta & Myrberg 2009). The benthic communities below the euphotic zone are dependent on the primary production from the upper water column as a food source, but the input of organic matter from the water column varies both spatially and temporally (Josefson et al. 2012). In addition, coastal seas are increasingly affected by multiple stressors, including eutrophication, climate change and invasive species.

Increased species and functional trait richness enhances ecosystem functioning as predicted by biodiversity–ecosystem -functioning theory (Balvanera et al. 2006). Invasive species are often considered to be a major threat to both aquatic and terrestrial ecosystems worldwide due to their potential effects on e.g. resource levels and community dynamics leading to possible competition with and changes in the native community (Mack et al. 2000, Ehrenfeld 2010), where also functioning of the communities may be altered. Invaders can, however, also have positive effects on the ecosystem they invade, depending on whether or not they increase or decrease the complexity or heterogeneity of the environment (Crooks 2002), or are, in other words, drivers or passengers of change in the community (MacDougall & Turkington 2005). Arrival of an invasive may also lead to an increase in the species and/or functional richness given that the species is invading an available niche and thus exploiting resources unused by the native community (Stachowicz & Byrnes 2006). Thus the functional contribution of non-indigenous species may be particularly strong in our study system, the Baltic Sea, which is vulnerable to species invasions due to its naturally low species richness and the frequent disturbances occurring in the system (Leppäkoski et al. 2002, Bonsdorff 2006).

The polychaete genus *Marenzelleria* spp. (Spionidae) was first observed in the southern Baltic Sea in 1985 (Bick & Burckhardt 1989), and in the study area in the northern Baltic Proper in 1990 (Norkko et al. 1993), and has since then spread to the entire Baltic Sea becoming the numerically dominant member of many benthic communities alongside the Baltic clam *Macoma balthica* (Linnaeus, 1758) (Kauppi et al. 2015). Three different species of the genus now occur in the Baltic Sea; *M. viridis* (Verrill, 1873) and *M. neglecta* Sikorski and Bick 2006 of North American origin (George 1966), and *M. arctia* (Chamberlin, 1920) of Arctic origin (Blank et al. 2008). All three species represent new functionality in the system through their

more active and deeper burrowing and bioirrigation compared to the native fauna, which possibly has an effect on ecosystem functioning in terms of nutrient cycling (Renz & Forster 2013, 2014). Because *Marenzelleria* spp. adds functional diversity (Hewitt et al. 2016), it is imperative to know how it modifies the surrounding ecosystem.

Marenzelleria spp. has been subject to many experimental and modeling studies regarding its potential effects on ecosystem functioning. Results from laboratory experiments are, however, seldom directly applicable in nature, where environmental conditions and the structure of animal communities vary both spatially and temporally. Studies on multiple scales, both spatial and temporal, are needed in order to identify feedback mechanisms and interactions important for ecosystem functioning, which might not be visible in short-term experiments (Lohrer et al. 2015). Our ability to predict changes in biodiversity and subsequent ecosystem functions and services is hampered by the lack of quantitative measures on the seasonal variability as well as the directional change of the drivers affecting ecosystem functions, such as the establishment of potentially functionally dominant species. Despite the well-known seasonal variation in temperature and food input to benthos, both important for nutrient cycling, temporal studies that quantify nutrient fluxes and account for the seasonally changing role of benthic macrofaunal community structure are exceedingly rare globally. Also studies directly quantifying the impacts of invasive species on ecosystem functions are scarce. This study was designed to explore the effects of the *Marenzelleria* species complex on an important ecosystem function, nutrient cycling, in the field in natural conditions in a seasonally changing environment. Recent studies in the Baltic Sea have addressed the contribution of macrofauna, including *Marenzelleria* spp., to nutrient dynamics in a spatial context and along hypoxic disturbance gradients (e.g. Norkko et al. 2015, Gammal et al. 2016), but the seasonal aspect remains poorly understood even in a well-studied system like the Baltic Sea.

The aims of this study were 1) to quantify seasonal differences in benthic fluxes of oxygen and inorganic nutrients and to assess 2) whether or not *Marenzelleria* spp. affect these fluxes, and 3) if the effect of *Marenzelleria* spp. varies seasonally and which other factors, such as temperature, organic matter content and C/N ratios in the sediment, influence the nutrient fluxes during different seasons. As seasonal differences in e.g. temperature were hypothesized to be more pronounced at shallower depths, we also investigated whether or not there were spatial differences with regards to depth in nutrient dynamics over the year. We also predicted that the effect of the biotic factors, in this case macrofauna, would have a greater effect on the fluxes during summer when temperatures are higher.

Methods

Study sites

We chose two sites with differing depths for the study, Storfjärden 33 m (59°51.316’N / 23°15.815’E), and Munken 10 m (59°51.105’N / 23°14.680’E) deep. Storfjärden is a typical outer archipelago accumulation bottom with mud as sediment type. It has a direct connection to the open sea and can experience large variation in hydrography due to upwelling events (Niemi 1973), increasing productivity by sediment resuspension and by bringing nutrient-rich water from deeper areas. Munken with mud mixed with a small proportion of fine-grained sand is situated within one kilometer from Storfjärden and represents a transportation site situated on the edge of a steep slope, where currents easily transport the sediment down to deeper areas and organic matter thus rarely accumulates. The summer thermocline affects water circulation at Storfjärden, but hypoxia occurs only rarely at the site. According to recent genetic analyses (Kauppi et al. unpublished data), the *Marenzelleria* spp. species present at Storfjärden is *M. arctia* and at Munken *M. neglecta*.

Sampling design

To study the effects of *Marenzelleria* spp. on the seasonal nutrient dynamics we conducted ship-based incubations of intact sediment cores to measure nutrient fluxes at the two sites.

Sampling was conducted monthly from early June 2013 until mid-June 2014, with the exception of December 2013 and February and April 2014 when sampling was not conducted due to challenging weather conditions (sea ice, storm). At the deeper site we were unable to retrieve any samples in September 2013 and only two replicate flux samples in March 2013 due to the loose sediment structure making it difficult to sample without disturbing the sediment surface. Temperature and salinity were measured with a CTD device at each sampling occasion (Falmouth Scientific NXIC CTD). At each sampling occasion, five replicate intact sediment cores for benthic flux incubations per site were retrieved in acrylic core liners with an inner diameter of 9 cm using a Gemax twin corer. The sediment height in the cores was approximately 30 cm with 15 cm of overlying water. Water samples for dissolved oxygen, NO_x (NO_2^-+ NO_3^-), NH_4^+, PO_4^{3-} and Si^{4+} (not analyzed in June and early July 2013), Fe_{tot} and Mn_{tot} (not analyzed in June and early July 2013) were taken at the start and end of the incubation from the overlying water in the cores. After the initial water sampling, cores were immediately closed with lids fitted with magnetic stirrers and the incubation started within minutes of the core retrieval. The cores were incubated in an incubation chamber filled with water at *in situ* temperature in darkness under constant stirring for 4 hrs. Stirring prevents the formation of solute gradients in the water column under the incubation. Oxygen samples were fixed with $Mn(II)SO_4$*4 H_2O and NaI, NaOH (aq). Nutrient samples were filtered through Whatman GF/F glass fiber filters and frozen until analysis of dissolved NO_x, NH_4^+, PO_4^{3-} and Si^{4+}. For iron and manganese samples, 30 ml of the filtered sample was fixed with 0.83 ml 65% HNO_3 (l) and stored at +4°C until analysis.

Two additional cores per site were retrieved for porewater and sediment samples. For the sediment samples, the top cm of the core was sliced and frozen for later analysis of organic content, grain size and sediment C/N –ratio. For porewater samples the core was sliced into 0-1, 1-2, 2-3, 5-6 and 10-11 cm sections. The sediment slices were centrifuged and the supernatant was filtered through Whatman GF/F filters and frozen for later analysis of NO_x, NH_4^+, PO_4^{3-} and Si^{4+}.

After incubation, the top 1 cm of each core was sieved separately through a 0.2 mm mesh to retrieve juvenile and newly settled fauna. The rest of the core was sieved through a 0.5 mm mesh. The faunal samples were stored in 70 % EtOH and stained with rose Bengal. Macrofauna were identified to the lowest possible taxonomic level and biomass was measured as wet weight of blotted animals.

Analyses

Solute fluxes

Oxygen samples were analyzed by Winkler titration. Water column and porewater solutes were analyzed at Tvärminne Zoological Station (Thermo Scientific Aquakem 250). Quantification limits for solutes were NH_4^+ 0.0001, NO_x 0.00003, PO_4^{3-} 0.00003 and Si^{4+} 0.0007 mmol/l. Solute fluxes were calculated from the difference in the concentration between start and end samples as mmol/m^2*d.

Iron and manganese affect phosphorus cycling in the sediment, and are therefore important for nutrient dynamics. Oxygen flux into the sediment controls the reactions of these at the sediment–water -interface, and needs to be maintained as close to natural *in situ* -flux as possible for correct measurement (Sundby et al. 1986). The oxygen concentration inside the flux chambers was allowed to decrease following respiratory activities of the benthic

community. However, the oxygen concentration never dropped below 31.6 % saturation, thus not affecting e.g. the behaviour of the fauna. Iron and manganese concentrations of the samples were measured with ICP-MS (Agilent 7500ce with Octopole reaction system, helium was used as the reaction gas) and MP-AES (Perkin Elmer MP4200 AES). Iron was measured with isotope Fe-56 and manganese with isotope Mn-55. Because of the salinity of the seawater, samples were diluted to 1:10 and High Matrix Introduction (HMI) was used. Quantification limit with ICP-MS for iron was 2.4 ppb and for manganese 6.4 ppb. Error for iron was 8 % and for manganese 7 %. Analysis method was changed to Perkin Elmer MP4200 AES after January 2014 because the salts in the seawater clogged the sample loop and further dilution would have resulted in amounts of Fe and Mn under the detection limit and a considerable uncertainty in the results. Wavelength for iron was 371.993 nm and for manganese 403.076 nm. Samples analyzed with MP-AES were not diluted. Quantification limit with MP-AES for iron was 2.5 ppb and for manganese 1.0 ppb. Error for iron was 7 % and for manganese 5 %.

Sediment analyses

Organic matter content of the sediment was determined as loss on ignition (LOI %). The samples were first dried at 60°C for 48 h and thereafter combusted at 500°C for 3 h. For grain size analysis, sediment was first placed in 6% hydrogen peroxide –solution to remove the organic matter. Thereafter the sediment was sieved through a series of sieves (0.063, 0.125, 0.25, 0.5, 1 and 2 mm), the different fractions were dried at 60°C for 48 h or until dry, and the dry weights of the fractions were measured. The C/N -ratio of the sediment was analyzed at Tvärminne Zoological Station with a Europa Scientific ANCA-MS 20-20 15N/13C mass spectrometer after removal of carbonates from the sediment with HCl (aq).

Statistical analyses

The contribution of biological factors (abundance of *Marenzelleria* spp., *Macoma balthica* and others (i.e. all other taxa combined) and environmental factors (temperature, salinity, pH, LOI, C/N -ratio) for predicting the variation in oxygen and solute fluxes was studied multivariately using distance-based linear modelling (DistLM). DistLM (Distance-based linear models in PERMANOVA+ for PRIMER 6, Anderson et al. 2008) are multiple regression models on multivariate response data that partition the variance explained by a set of predictor variables. By analyzing all fluxes simultaneously this model can provide a comprehensive understanding of the factors affecting organic matter degradation processes (e.g. Belley et al. 2016, Gammal et al. 2016). Biomass was measured as blotted wet weight and only the largest specimens of *M. balthica, Marenzelleria* spp., *Hediste diversicolor, Monoporeia affinis, Hydrobia* spp. and *Paludestrina jenkinsii* had a detectable weight. Wet weight is also subject to a large variability due to the water retained in the animals. For a large number of animals, e.g. juveniles, there will be no measurable biomass, which causes us to lose some of the seasonal variation in this measure. We did run the analysis also with biomass as predictor, but this did not add explanatory power to the analysis. Abundance, therefore, is a more accurate measure in this case. For the DistLM analysis, distance matrices based on pairwise Euclidean distances between samples were constructed of the response fluxes combined together (NO_x, NH_4^+, PO_4^{3-}, Si^{4+}, Fe, Mn and O_2) after normalizing. The combined flux gives the best general picture of the effect of seasonality on nutrient dynamics. After initial visual inspection of the environmental data over the whole year, the data was divided into two datasets according to the changes in oxygen consumption, which can be used a proxy for the activity of the fauna and the microbial processes in the sediment (Glud 2008). We chose two periods, one of low and one of high consumption (hereafter low and high), respectively, and ran a PERMANOVA analysis with month as a factor (PERMANOVA+ for PRIMER 6.0 Anderson et al. (2008)) to test whether the seasons actually significantly differed from each other. The pattern of oxygen

consumption differed between the sites, such that at the deeper site, the period of high oxygen consumption ended in late July whereas at the shallower site it ended in August. Additionally, NMDS graphs (Figure S1 in electronic supplements) of the macrofauna community and solute fluxes suggested a gradual transition from low to high oxygen consumption during March and May, which was separated as their own period. Separate DistLM -analyses were then run for the entire year, and low, high oxygen consumption and March and May separately. Silicate and manganese were omitted from the combined flux variable in the analyses of the entire year and high season due to lack of data from the first two months. Significant variables from both sets of predictors (biological and environmental) were first chosen independently through forward selection, and after combining the two sets of predictor variables, the significant variables from the independent selections were forced into the model first and the program then selected any other variables to be included in the model through both forward and backward selection. If there were no significant predictors in neither set of predictors, all predictors were trialed together using both forward and backward selection. Akaike Information Criterion (AIC) was used as the model selection criterion, and the model with lowest AIC was chosen. Both marginal tests, testing the effect of the independent predictor variables on the response variable, and sequential test testing the effect of all chosen predictors on the response variable, were run. Correlation matrices between the predictors and individual response variables are presented in table S4 in electronic supplements. Based on the inspection of draftsman and sd to mean –plots as suggested in Clarke and Warwick (2001), a $\sqrt{(x+1000)}$ -transformation was applied to the fluxes of NO_x, NH_4^+, PO_4^{3-} and Fe at Storfjärden. None of the other fluxes required transformations at either of the sites. The predictor variables are automatically normalized in the DistLM -analysis. The only highly correlated predictor variables after normalizing were the abundance of *Macoma* and the abundance of other species and salinity and pH at Storfjärden (0.78 and -0.77, respectively). These were nevertheless left in the analysis untransformed since omitting or transforming them did not significantly affect the results.

Results

Environmental parameters

The environmental variables exhibiting greatest variation between the seasons were temperature, bottom-water oxygen content and sediment organic matter content measured as LOI % (Table S2 in electronic supplements). The minimum temperature measured in March was similar for both sites (2.1 °C at Munken and 1.9 °C at Storfjärden). The maximum temperature, however, was nearly five degrees higher at Munken (14.0 °C) than at Storfjärden (9.1 °C) and was measured at Storfjärden in June 2013 and 2014, and at Munken in September 2013. The maximum (12.8 mg/l and 12.5 mg/l for Munken and Storfjärden, respectively) and average (10.3 and 9.1 mg/l for Munken and Storfjärden, respectively) dissolved oxygen content in the bottom water at both sites were almost identical, but the sites differed in the minimum oxygen content (8.5 and 5.0 mg/l for Munken and Storfjärden, respectively). Even the minimum value at the deeper site was nevertheless up to two-fold higher than the limit for hypoxia (2 mg/l DO, Diaz & Rosenberg 2008), under which we could expect severe hampering in the functioning of the macrofaunal community. The average organic content of the sediment was several percent higher at Storfjärden (13.9 %) than at Munken (8.9 %) (Table S2), and differences in the organic content between months were much larger at Munken than at Storfjärden, where the values were relatively stable over the whole year (min and max 5.5 to 12.5 % and 12.8 to 15.3 % for Munken and Storfjärden, respectively).

Abundance and biomass of Marenzelleria *spp. and other macrofauna*

At both sites the changes in the abundance of the macrofauna followed a similar pattern with a peak in the total abundance in late July and August. Apart from the dominating *Marenzelleria* spp. and *M. balthica,* the other species observed at Munken were *Halicryptus spinulosus, Microstomum lineare, Hydrobia* sp., *Paludestrina jenkinsi, Manayunkia aestuarina, Hediste diversicolor, Cerastoderma glaucum, Limapontia capitata, Theodoxus fluviatilis, Cyanophthalma obscura,* Oligochaeta, Chironomida and Nemertea. At Storfjärden other species observed include *Bylgides sarsi, Monoporeia affinis, Microstomum lineare,* Oligochaeta, Chironomida, and Nemertea. Also a few sporadic *Saduria entomon, Idotea baltica, Mya arenaria, Mytilus edulis* and *Mysis* sp. were observed at one or both sites but were not included in the analysis.

Munken had a higher average total abundance than Storfjärden, but the community was mainly dominated by juveniles of different species and smaller-sized, more opportunistic species such as Oligochaeta and chironomids. The dramatic increase in total abundance at Munken (Fig. 1 a) in late July and August was caused by the increase in the number of settling juvenile *M. balthica* and Oligochaeta. The peaks in total abundance at Storfjärden in July, August and September (Fig. 1 b) were a consequence of both settling *M. balthica* and a seasonally increasing total number of species contributing to the total abundance. A notable difference in the community composition between the sites was the population dynamics of *Marenzelleria* spp. At Munken there was a clear peak in the abundance of *Marenzelleria* spp. in March and May, caused by the settling juveniles, whereas over the rest of the year, *Marenzelleria* spp. only occurred sporadically at this site (Fig. 1 a). At Storfjärden there were no clear peaks in *Marenzelleria* spp. abundance, rather it occurred at the site over the year, with a slight increase from June to August also due to settling juveniles (Fig. 1 b). The numerically most dominant taxa at both sites were *M. balthica* and *Marenzelleria* spp. Lowest abundances of *M. balthica* occurred at Storfjärden (mean 1289 ind/m^2) and at Munken (mean 1886 ind/m^2) in June 2013. Highest abundances of *M. balthica* occurred at Storfjärden and Munken in late July 2013 (8174 and 51244 ind/m^2, respectively). Lowest abundances of the second-most abundant taxa, *Marenzelleria* spp. were observed at Storfjärden in January 2014 (mean 912 ind/m^2) and at Munken in late July, September and October 2013 (mean 63 ind/m^2 at each sampling occasion), and highest abundances of *Marenzelleria* spp. were observed at Storfjärden (mean 3112 ind/m^2) and Munken (mean 17762 ind/m^2) in late July 2013 and May 2014, respectively. For monthly average abundances, see Table S2 in the electronic supplements.

Contrary to the relatively similar abundance patterns, the seasonal pattern of the macrofaunal biomass differed between the two sites (Fig. 1 c&d). At both sites, the species contributing most to the biomass was *M. balthica.* A clear difference was the much higher and more stable total biomass over the year at Storfjärden compared to the more seasonally variable pattern at Munken. The highest biomass at Storfjärden occurred in January 2014 (mean 308.9 g/m^2) and at Munken in August 2013 (mean 106.9 g/m^2). The lowest biomasses were measured in March 2014 (mean 113.0 g/m^2) at Storfjärden and in January 2014 (mean 0.2 g/m^2) at Munken. *Marenzelleria* spp. biomass was also more stable at Storfjärden than at Munken. The highest and lowest average biomass of *Marenzelleria* spp. at Storfjärden occurred in June 2014 (mean 9.2 g/m^2) and March 2014 (mean 1.5 g/m^2), respectively, and at Munken in early July 2013 (mean 0.01 g/m^2) and May 2014 (mean 6.9 g/m^2) (Fig. 1 c&d). For monthly average biomasses, see Table S2 in the electronic supplements.

Seasonal oxygen consumption of the sediment

The oxygen consumption of the sediment, including microbial and macrofauna respiration, at both sites varied during the year mostly following variations in the bottom-water temperature (Fig. 2 a&b). Highest oxygen consumption at Storfjärden (33 m) (Fig. 2 b) was measured in

June 2013 (35.9 ± 2.4 mmol $m^{-2}d^{-1}$, mean ± sd throughout) and at Munken (10 m) (Fig. 2 a) in early July 2013 (33.7 ± 12.9 mmol $m^{-2}d^{-1}$). At the deeper site this also corresponds to the highest bottom-water temperature measured over the study period (9.1°C). The lowest oxygen consumption rates at Storfjärden and Munken were recorded in November (11.5 ± 4.1 mmol $m^{-2}d^{-1}$) and January (9.3 ± 1.7 mmol $m^{-2}d^{-1}$), respectively. See Table S2 in the electronic supplements for monthly fluxes. According to the PERMANOVA -analysis, there was a significant difference between summer and winter in oxygen consumption at both sites (Storfjärden: Pseudo-$F_{1,44}$ = 173.4, p=0.0001; Munken: Pseudo-$F_{1,52}$ = 29.0, p=0.0001). Oxygen consumption was significantly lower at Storfjärden in the period from August 2013 to March 2014 (low) compared to other months (June 2013–late July 2013, May 2014–June 2014, high). At Munken, the oxygen consumption was significantly lower from September 2013 to March 2013 (low) compared to other months (June 2013–August 2013, May–June 2014, high). The average oxygen consumptions (mean±SD) during the different seasons defined for the DistLM analysis at Storfjärden were 30.6±3.4 mmol $m^{-2}d^{-1}$ (high) and 13.7±1.9 mmol $m^{-2}d^{-1}$ (low) and at Munken 24.8±6.9 mmol $m^{-2}d^{-1}$ (high) and 14.1±6.0 mmol $m^{-2}d^{-1}$ (low).

Seasonal solute fluxes across the sediment–water interface

Fluxes of all solutes (NO_x, NH_4^+, PO_4^{3-}, Si^{4+} and micronutrients Fe, Mn) demonstrated some degree of seasonal variation (Fig. 3 & 4). Generally there was an efflux of all the inorganic solutes at Storfjärden (Fig. 3 b, d, f, h) over the year, except for phosphate (Fig. 3 f), which showed an influx in October 2013 and March 2014, and iron (Fig. 4 b), which showed an influx from November 2013 to June 2014, and NO_x (Fig. 3 b), which showed an influx in October and November 2013. At Munken, the shallower site, the fluxes of inorganic solutes were overall smaller than at the deeper site and their direction varied over the year for all fluxes (Fig. 3 a, c, e, g) except Si^{4+} (Fig. 3 g), which was always diffusing out from the sediment. Monthly fluxes of all solutes (mean±sd) are presented in Table S2 in the electronic supplements. See Fig. S3 in electronic supplements for porewater and bottom-water concentrations over the year.

Factors predicting seasonal variation in the combined solute flux

According to the DistLM results, the best model could account for 57 % of the total variation of the combined flux at Storfjärden (33 m) and 25 % at Munken (10 m) over the whole year (Table 1). The most important predictor variables in the model at the deeper site were organic matter content, the abundance of *Marenzelleria* spp., temperature and C/N -ratio. At the shallower site the most important predictor variables in the model were salinity and temperature.

After investigating the contribution of predictor variables for the whole year, the model was then run for low and high season, and March+May separately. During low season at Storfjärden (33 m) only the C/N -ratio was a significant predictor for the fluxes accounting for 19 % of the total variance explained. Overall the model could account for 40 % of the variation in the combined flux with temperature and *Marenzelleria* spp. also being selected into the model. Backward selection of the predictor variables additionally resulted in salinity, pH and organic content to be included in the model but with a lower AIC-value. At Munken (10 m) pH was the only significant predictor in the model during low season. The other predictor variables selected into the model were temperature, salinity, C/N -ratio, abundance of *Macoma* and abundance of *Marenzelleria* spp. and these together with pH accounted for a total of 49 % of the variation in the combined flux. *Marenzelleria* spp., although not significant in the overall model, accounted for 15 % of the total explained variation. In the marginal tests, *Marenzelleria* spp. alone was a significant predictor of the combined flux accounting for 19 % of the variation.

During the high season at Storfjärden (33 m) temperature and organic content were the only significant contributors in the model and could together account for 45 % of the variation in the combined flux (Table 1). Alone, however, the organic content could only account for a non-significant 1.6 % of the total variation. According to the marginal test *Marenzelleria* spp. could alone account for a non-significant 8 % of the total variation (Table 2). At Munken (10 m) during high season salinity and the abundance of *Marenzelleria* spp. were the only significant predictors for the combined flux, of which 41 % could be accounted for with the final model. Other predictors included were temperature and organic content. In the marginal tests *Marenzelleria* spp. accounted for a non-significant 4 % of the variation in the combined flux.

The results from the DistLM analysis for March and May (Table 1), however, indicated a strong effect of the dominant macrofauna on the variation in the combined fluxes during this period. At Storfjärden the abundance of the fauna could account for in total 92 % of the variation, and the proportion of *Marenzelleria* spp. was 62 % and *Macoma* 30 % of the total explained variation. At Munken the fauna could account for 84 % of the variation and *Marenzelleria* spp. and the abundance of other taxa were significant predictors. *Marenzelleria* spp. accounted for 43 % and the abundance of other fauna for 10 % of the total explained variation, whereas *Macoma* accounted for 31 % of the total explained variation, but was not a significant predictor.

According to the results from the marginal tests *Marenzelleria* spp. significantly predicted the variation in the combined flux at Storfjärden during the whole year and in March and May, and at Munken in winter (Table 2). The other dominant species at the sites, *Macoma balthica*, was alone not a significant predictor of the combined flux during any time period.

Discussion

We demonstrate seasonal variation in benthic fluxes across the sediment–water -interface at two adjacent coastal locations: a deep depositional site, Storfjärden (33 m), and a shallow transportation site, Munken (10 m) in the northern Baltic Sea. There is a clear seasonal pattern in the oxygen consumption at both sites suggesting seasonality in the activity of the sediment-dwelling organisms (Michaud et al. 2005, Glud 2008). Decreased oxygen consumption also corresponds to decreased fluxes of all inorganic nutrients at Storfjärden, which indicates that the rates of sediment processes are linked to nutrient remineralization at the deeper site. Also phosphate fluxes show clear seasonal pattern with much lower fluxes during low season at this site. At the shallower site the pattern of nutrient dynamics over the year is similar to the deeper site but the fluxes overall are negligible. Oxygen uptake and solute flux results are similar to results obtained in other studies in this area (Norkko et al. 2015, Gammal et al. 2016). Importantly, results from the DistLM analyses, although correlative, emphasize the role of the invasive polychaete genus *Marenzelleria* spp. in spring at both sites, likely connected to their role in processing the organic matter settling after the spring bloom (Heiskanen & Tallberg 1999). *Marenzelleria* spp. was also a significant predictor of the combined solute flux at the deeper site during the whole year, but also contributed to explaining the variance during the period of low oxygen consumption. At the shallower site its contribution was less during the year as expected by the lower abundances, but even at this site the worms were important during spring accounting for 43 % of the variation in the fluxes, and, slightly surprisingly, during winter accounting for 18 % of the variation according to the marginal tests and also in the overall model. Apart from the high numbers of juvenile *Marenzelleria* spp. settling at the shallower site in March and May, the specimens found at this site are mostly very large individuals of *M. neglecta*, which could affect nutrient cycling more through their temporally more stable biomass, burrow structure and activity (Aller 1980a). The other dominant species, *Macoma balthica*, did predict the variation in the combined flux in March and May at both

sites, but otherwise its contribution for predicting the variation in the combined flux was not significant.

Variable food input modulates the impact of benthic fauna

Temperature affects the activity of macrofauna and microbial processes, and the movement of solutes in porewater, thereby directly affecting nutrient fluxes. Organic matter availability affects the activity of the macrofauna and microbes, and provides the raw material for the mineralization processes (e.g. Moodley et al., 2005). The variation in organic matter content and temperature had an overriding importance for predicting the variation in the combined flux compared to the fauna during our defined summer season at the deeper, more organic-rich, site. This is probably because we excluded silicate and manganese fluxes from the combined flux during this period due to the lack of data, since these two fluxes have high positive correlations with the fauna during the time of high oxygen consumption.

However, the highest oxygen consumption and fluxes of inorganic nutrients do not coincide with the highest faunal abundances and biomasses. This indicates that a high density of animals does not directly equal high levels of nutrient remineralization, but the activity needs to be somehow triggered. In temperate soils, for example, the activity of the microbial biomass is triggered by increasing temperatures, even though the size of the microbial biomass may remain constant (Blume et al. 2002). In aquatic systems, previous studies on the effect of seasonality on nutrient dynamics have identified temperature, and organic matter quantity and quality as important factors affecting benthic fluxes (Rysgaard et al. 1998, Witte et al. 2003, Moodley et al. 2005, Braeckman et al. 2010). However, the links between seasonal variability in environmental conditions, the macrobenthic and microbial communities, and ecosystem functioning are rarely studied together resulting in incomplete knowledge of their interactions. Knowledge of these interactions is increasingly important as the predicted ocean warming is likely to have impacts on the variation in the environmental drivers affecting the benthic fluxes.

Organic matter is ultimately remineralized by the microbial community in the sediment, the activity of which is stimulated by the bioturbation of macrofauna (Braeckman et al. 2010, Foshtomi et al. 2015). Microbial community composition at the study sites is shaped by oxygen availability and organic matter quality varying seasonally (Vetterli et al. 2015). In the archipelago zone in our study area the highest sedimentation rates occur during the dinoflagellate and diatom-dominated spring bloom (Tamelander & Heiskanen 2004), followed by lower sedimentation rates during summer and increased resuspension during autumn (Heiskanen & Tallberg 1999). Bioirrigation enhances the diffusion of dissolved silica out of the sediment and also the dissolution of biogenic silica into the porewater (Marinelli 1992). The slight increases in the silicate fluxes measured at Storfjärden and Munken in October and November 2013 and in May 2014 are thus probably a consequence of the recycling of silicate from the sedimenting organic matter.

Seasonal patterns are site-dependent

The natural seasonal variability in environmental conditions translates into similar patterns of nutrient dynamics, but with different magnitudes between sites. The factors driving the variation in nutrient fluxes also differ and overall there is more variation left unexplained at the shallower site. The higher effluxes of all inorganic nutrients and influxes of oxygen at Storfjärden compared to Munken can be explained by higher organic content and abundance of fauna, especially actively burrowing *M. arctia* and an abundant and stable population of large-bodied, long-lived animals, in this case mostly *M. balthica*. Large-bodied, long-lived animals are important for the stability and functioning of ecosystems and their loss through e.g.

disturbances leads to impaired functioning (Thrush et al. 2006, Godbold & Solan 2009, Norkko et al. 2013). The stability in the ammonium fluxes at Storfjärden over the year is probably related to the stability in macrofaunal community composition. The seasonal importance of biologically or physically controlled processes for nutrient fluxes depends on the organic matter input stimulating the *potential* biogenic processes, of which follows the demonstrated increased nutrient fluxes in summer due to biogenic stimulation of nutrient remineralization especially at the deeper site.

At the shallower site, on the contrary, physically controlled processes driving sediment and fluid transport likely dominate over biologically controlled processes whenever organic matter is not available due to the site being inhabited by more short-lived, small animals (Aller 1980b, a). The patchiness of the fauna in both space and time at the shallower site together with the variability in the hydrodynamic conditions could thus be the reason for the large variability in the fluxes at this site. Temperature, and especially salinity were always selected as predictors into the model at Munken indicating that occasional upwelling and freshwater input from the nearby Pojo Bay have an effect on the fluxes at this site. Upwelling events and thermally-induced total circulation of the water masses also increase resuspension. Increased temperature, salinity and organic content in October after an upwelling event could have caused the slightly increased effluxes of ammonium, phosphate and silicate in November. The increased resuspension and sedimentation of organic matter possibly enhanced the activity of suspension feeding macrofauna hence the somewhat surprising importance of *Marenzelleria* spp. in predicting the fluxes during low season at both sites.

During the year the DistLM -model also had a low predictive power at the shallow site, with salinity and temperature the only selected predictors. We cannot see a clear seasonal difference in the fluxes of all the inorganic nutrients despite a seasonal pattern in the organic content and in the oxygen fluxes, but whenever organic matter is available, or the fauna is very abundant, the biotic factors seem to be of value in predicting the fluxes. For instance the high predictive value and significance of *Marenzelleria* spp. and other macrofauna at the shallower site from March to June coincides with an increase in the organic matter and is probably partly due to the high negative correlations these have with the NO_x -fluxes added to the high positive correlation *Marenzelleria* spp. has with iron and manganese fluxes. Nitrification is affected by the availability of oxygen and ammonium, organic matter and temperature. At the study sites nitrification rates have previously been found to be highest during summer, when ammonium availability following mineralization of organic matter is high (Jäntti et al. 2011). This could partly explain the NO_x -pattern at the shallower site, with efflux from August to October, when also ammonium -effluxes are high indicating high ammonium availability. In addition to seasonal variability in nutrient dynamics within both sites, we thus also have a relatively large spatial variability between sites less than one kilometer apart, with much lower fluxes overall at the shallower site, owing in part to the differences in the biological components of these sites.

Marenzelleria *spp. has an important role in nutrient cycling*

The invasive polychaete *Marenzelleria* spp. has increased species and functional richness in the Baltic Sea (Hewitt et al. 2016). While invasive species might increase the richness in some systems, little is known about how this might affect ecosystem functioning (Gamfeldt et al. 2015). *Marenzelleria* spp. has been suggested to be a driver of ecological change in the Baltic Sea helping in the mitigation of eutrophication and thereby providing important ecosystem services (Norkko et al. 2012). High abundances of *Marenzelleria* spp. could potentially have positive effects on nutrient cycling in the Baltic Sea, as their oxygenation in the long term could bind phosphorus and thus prevent its release to the water column (Hietanen et al. 2007, Norkko et al. 2012). Phosphorus can be removed from the water through adsorption onto clays

and on both iron and manganese oxyhydroxide particles in well-oxygenated sediment (Föllmi 1996). On the other hand, burrowing deep into the anoxic sediment could cause oxygen-depleted, sulfide and nutrient-rich water to be transported to the sediment surface, and thereby boost primary production and eutrophication (Quintana et al. 2011). Counteracting hypoxia and reducing phosphorus and nitrogen fluxes into the water column play an essential role in mitigation of eutrophication, a pertinent problem in the Baltic Sea as well as many other estuaries (Carstensen et al. 2014). Our findings clearly suggest that *Marenzelleria* spp. does have an effect on nutrient cycling also in natural conditions, but it varies according to the site, season, and also depending on the nutrient species in question. During the low season the effect of the worms may be low and non-significant, but the effect of even a moderate density of worms can be substantial when there is organic matter to be ingested and processed. The finding that *Marenzelleria* may have the strongest effect after the spring bloom is corroborated by the findings by Josefson et al. (2012) and Norkko et al. (2015). The high predictive value of macrofauna after the spring bloom and the significance of *Marenzelleria* spp. is demonstrated also in both good and poor oxygen conditions (Norkko et al. 2015), further supporting the important role of the fresh food supply to the system and highlighting the role of the invasive polychaetes and macrofauna in general in processing this organic matter.

Accumulation of organic matter in the sediment increases the internal nutrient recycling and can thus promote eutrophication. The effect of *Marenzelleria* spp. on nutrient cycling could also be more indirect in character by mainly enhancing organic matter processing rate and efficiency. *M. arctia* can enhance resource utilization through resource partitioning compared to the native fauna (Karlson et al. 2011, Karlson et al. 2015). Our observations of highly stable organic matter content at Storfjärden compared to what e.g. Jäntti et al. (2011) found at the same sites could be an indication of the benthic community including *M. arctia* being so efficient at utilizing the settling material, that spring and summer blooms are not visible as peaks in the organic content. The low sampling interval during this period possibly lead to a failure in detecting the peak, as the settling organic material is potentially processed very fast by the macrofauna deprived of food after the winter (e.g. Cederwall & Elmgren 1990). The much higher (maximum 31 %) and more variable organic matter content observed in the previous studies also coincided with much lower abundances of *Marenzelleria* spp. and other macrofauna potentially leading to inefficient resource use and accumulation of excess organic matter towards the end of the summer.

Conclusions

Modeling of nutrient budgets is often based on results obtained from experiments or field surveys conducted in the warm summer months. Evidence for seasonality in fluxes has, however, been piling up from different systems (Rysgaard et al. 1998, Moodley et al. 2005). Our results also clearly demonstrate seasonal variability in nutrient dynamics. This variability is partly due to seasonal variability in the structure and activity of the sediment-dwelling community responsible for the remineralization of organic matter. The seasonal differences in the activity of the fauna are due to seasonal changes in organic matter input and temperature. Furthermore, although the seasonal pattern in the fluxes at our accumulation and transport bottoms was similar, there were large differences in the magnitude of the measured fluxes and in the importance of different drivers. This highlights the importance of actually measuring nutrient fluxes *in situ* at varying spatial and temporal scales. Experiments are and will be needed to test the causes behind the effects, but upscaling to real-world ecosystem functioning is problematic due to short duration, highly simplified assemblages and manipulated sediments the experiments often are conducted in, omitting the natural variability (Snelgrove et al. 2014). When striving for generalizations we must not rely solely on data from short-term experiments, nor on studies done at one point of time albeit on a large spatial scale, but to combine these

results with ones incorporating temporal variability for a more complete picture of nature. Using data from short-term experiments conducted in summer when rates of processes and nutrient effluxes are at their maximum when calculating nutrient budgets could cause a gross overestimation in the calculations. Using data from only a month later, on the other hand, could cause a major underestimation. In both cases the estimates would not be realistic. Models are always simplifications of reality, but not including such a fundamental characteristic of the system as macrofauna and seasonality in them makes their use in management decisions doubtful.

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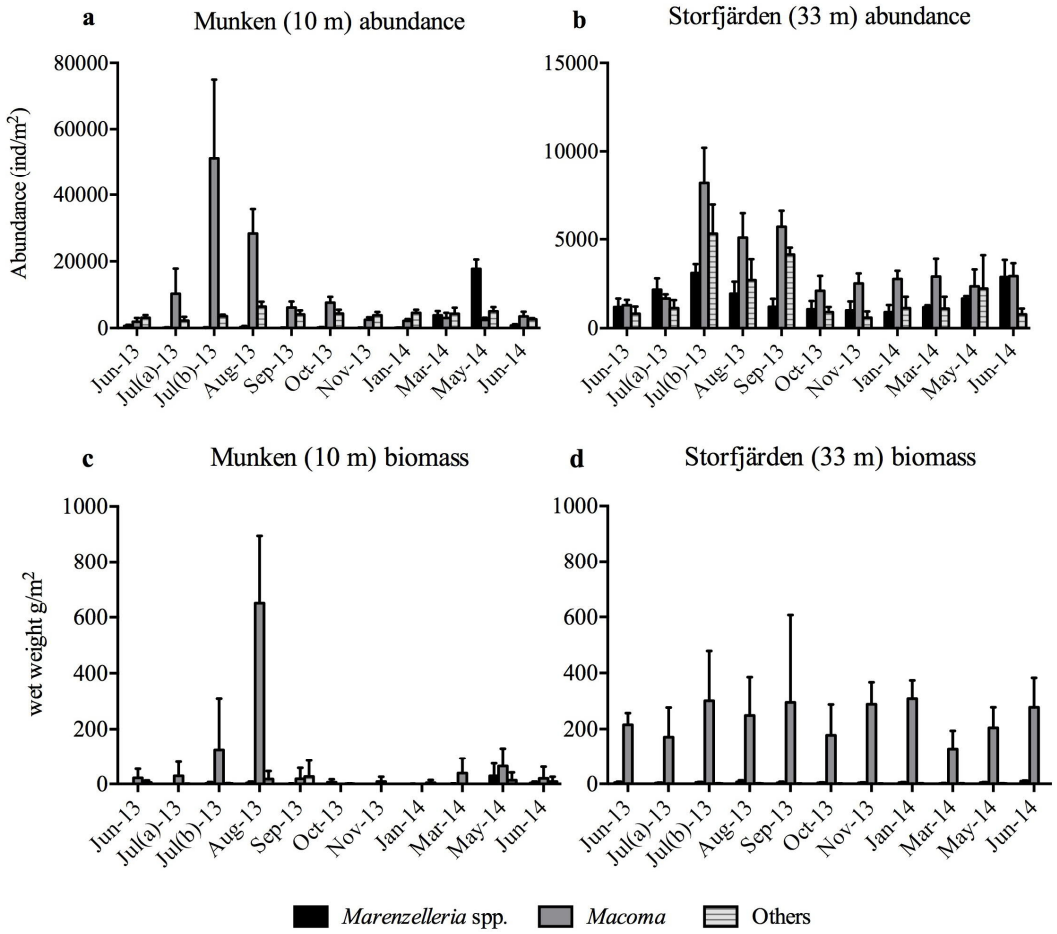

Fig. 1. Abundances and biomasses (mean±SD) of *Marenzelleria* spp. (black bars), *M. balthica* (grey bars) and others (striped bars) at the study sites Munken (a and c) and Storfjärden (b and d) from June 2013 to June 2014. Note the difference in the scale of y-axes of abundance at Munken and Storfjärden.

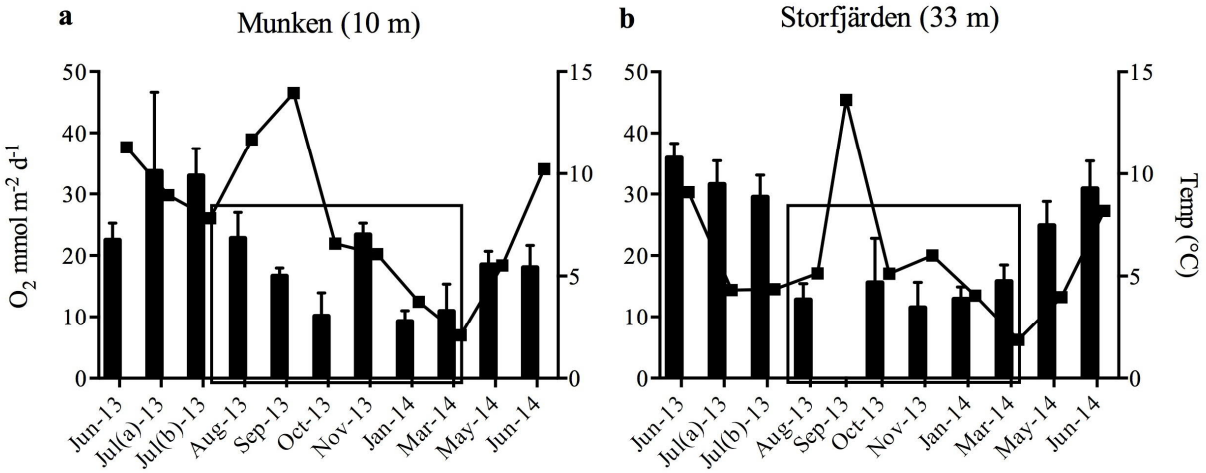

Fig. 2. Oxygen consumption (bars) (mmol/m^2*d) and bottom-water temperature (°C) (filled squares) at Munken (a) and Storfjärden (b) from June 2013 to June 2014. Bars represent the average consumption and error bars the standard deviation of five replicates, except for March 14 at Storfjärden (2 replicates). The square indicates the winter season as used in the DistLM analysis.

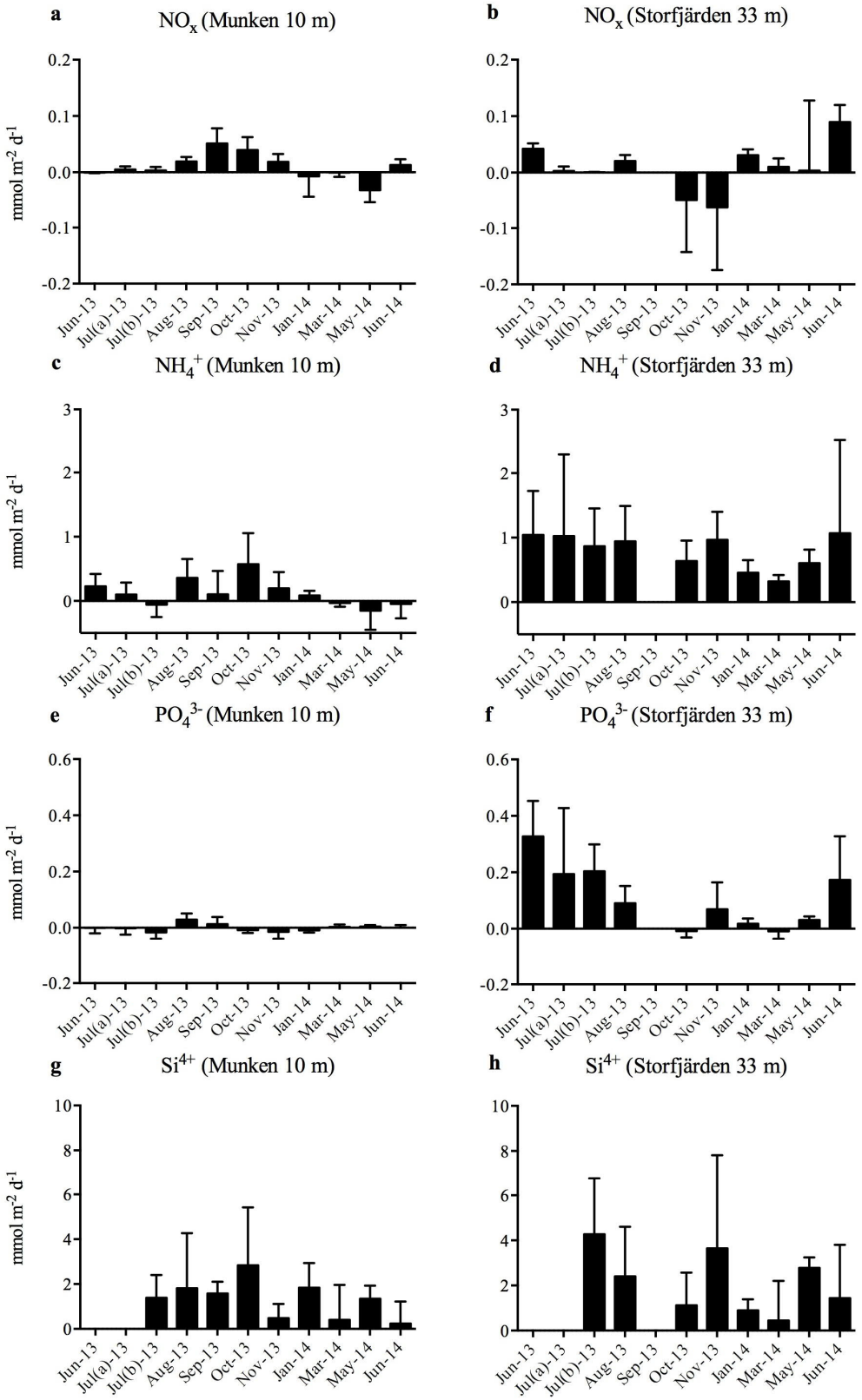

Fig. 3. Fluxes of NO_x, NH_4^+, PO_4^{3-} and Si at Munken (a-d) and Storfjärden (e-i) from June 2013 to June 2014. Grey bars represent the average flux, the error bars indicate standard deviation of five replicates, except for March 14 at Storfjärden (2 replicates).

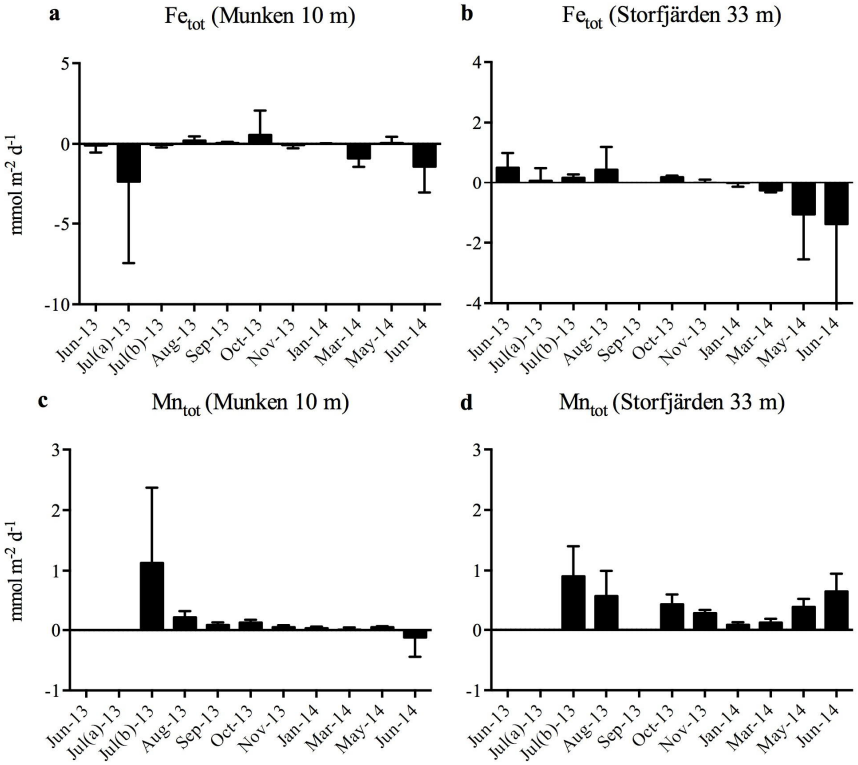

Fig. 4. Fluxes of Fe and Mn at Munken (a and b) and Storfjärden (c and d) from June 2013 to June 2014. From June 2013 to November 2013 samples were analyzed using ICP-MS and from January 2014 onwards using MP-AES. Grey bars represent the average and the error bars standard deviation of five replicate fluxes, except for March 14 at Storfjärden (2 replicates).

Table 1. DistLM results of the sequential tests for the final models of the combined flux as the response variable during the whole year, summer (high oxygen consumption), winter (low oxygen consumption) and March+May. AIC=Akaike Information Criterion, Cumulative R^2=proportion of variance explained by the model. Asterisks indicate *p*-values: *<0.05, **<0.01, ***<0.0001. OM=organic matter, Others=the total abundance of macrofauna other than *Marenzelleria* and *Macoma*.

Site	***Season***	***Predictor***	***AIC***	***Cumulative R^2***
Storfjärden (33 m)	*Year*	*OM***	516.6	0.30
		*Marenzelleria**	512.5	0.38
		*Temp**	509.6	0.45
		*C/N***	504.8	0.52
		Others	504.2	0.55
		Macoma	**503.9**	**0.57**
	high	*Temp***	236.6	0.26
		*OM***	**231.4**	**0.45**
	low	*Temp*	343.9	0.14
		Marenzelleria	343.8	0.21
		*C/N**	**339.7**	**0.40**
	March+May	*Marenzelleria**	85.1	0.62
		*Macoma**	**78.0**	**0.92**
Munken (10 m)	*Year*	*Salinity***	737.2	0.11
		*Temp***	732.4	0.21
		Marenzelleria	**731.9**	**0.25**
	high	*Salinity***	407.8	0.19
		Temp	407.5	0.25
		*Marenzelleria**	405.13	0.35
		OM	**404.1**	**0.41**
	low	*Temp*	363.8	0.03
		Salinity	362.2	0.17
		C/N	364.1	0.17
		Macoma	366.1	0.17
		Marenzelleria	363.7	0.31
		*pH***	**358.5**	**0.49**
	March+May	*Macoma*	144.2	0.31
		*Marenzelleria***	136.6	0.74
		*Others**	**133.6**	**0.84**

Table 2. Marginal test results for the dominant benthic species *Marenzelleria* spp. and *M. balthica* from the DistLM analyses with *Marenzelleria* spp. and *M. balthica* as a predictor variables and the combined flux as the response variable. Significant results are indicated in bold.

Site	***Season***	***Variable***	***Pseudo-F***	***P***	***Prop.***
Storfjärden	*Year*	***Marenzelleria***	**10.12**	**0.003**	**0.19**
		Macoma	0.18	0.67	0.004
Storfjärden	*high*	*Marenzelleria*	1.78	0.19	0.08
		Macoma	1.58	0.22	0.07
Storfjärden	*low*	*Marenzelleria*	1.36	0.26	0.06
		Macoma	0.02	0.90	0.001
Storfjärden	*March+May*	***Marenzelleria***	**6.59**	**0.04**	**0.62**
		Macoma	0.006	0.96	0.002
Munken	*Year*	*Marenzelleria*	0.56	0.47	0.01
		Macoma	1.76	0.16	0.03
Munken	*high*	*Marenzelleria*	1.06	0.27	0.04
		Macoma	1.30	0.22	0.04
Munken	*low*	***Marenzelleria***	**5.10**	**0.03**	**0.19**
		Macoma	1.09	0.32	0.05
Munken	*March+May*	*Marenzelleria*	2.03	0.16	0.20
		Macoma	3.66	0.07	0.31